



## **River connectivity reestablished: effects and implications of six weir removals on brown trout smolt migration**

**Birnie-Gauvin, Kim; Candee, Martin Milton; Baktoft, Henrik; Larsen, Martin Hage; Koed, Anders; Aarestrup, Kim**

*Published in:*  
River Research and Applications

*Link to article, DOI:*  
[10.1002/rra.3271](https://doi.org/10.1002/rra.3271)

*Publication date:*  
2018

*Document Version*  
Peer reviewed version

[Link back to DTU Orbit](#)

*Citation (APA):*  
Birnie-Gauvin, K., Candee, M. M., Baktoft, H., Larsen, M. H., Koed, A., & Aarestrup, K. (2018). River connectivity reestablished: effects and implications of six weir removals on brown trout smolt migration. *River Research and Applications*, 34(6), 548-554. <https://doi.org/10.1002/rra.3271>

---

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

**River connectivity reestablished: effects and implications of six weir removals on brown trout  
smolt migration**

*Accepted for publication in River Research and Applications*

Kim Birnie-Gauvin<sup>1</sup>, Martin M. Candee<sup>1,2</sup>, Henrik Baktoft<sup>1</sup>, Martin H. Larsen<sup>1,3</sup>, Anders Koed<sup>1</sup>, Kim  
Aarestrup<sup>1</sup>

<sup>1</sup> DTU AQUA, National Institute of Aquatic Resources, Section for Freshwater Fisheries Ecology,  
Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark

<sup>2</sup> Freshwater Biology, University of Copenhagen, Universitetsparken 4, 2100 København Ø, Denmark

<sup>3</sup> Danish Centre for Wild Salmon, Brugsådsvej 15, DK-8960, Randers SØ, Denmark

Author for correspondence: K. Birnie-Gauvin

kbir@aqua.dtu.dk

**Running title: weir removal effects on smolts**

## Abstract

Today's river systems have been extensively modified, requiring us to rethink how we approach the management of these important ecosystems. We evaluated the effects of removing six weirs in River Villestrup (Jutland, Denmark) on the smolt run of brown trout (*Salmo trutta*) over the course of 12 years. During five of these years, we evaluated the number, size and timing of smolts during their downstream migration. We found a significant increase in smolt output following the weir removals, along with a decrease in average length and indications of an earlier peak migration. Our results suggest that barrier removal has perhaps led to an increase in spawning success by adults, fry survival, recruitment, and smolt migration success. Weir removal is therefore a viable management approach to restore connectivity in freshwater streams and rivers, which promotes the passage of smolts as they migrate to marine environments.

**Keywords:** barriers, freshwater ecosystems, migration, removal, river restoration, *Salmo trutta*, smolt

## 47 **1. Introduction**

48

### 49 *1.1 River connectivity*

50 The diversity, abundance and sustainability of aquatic species have long been threatened by the human-  
51 induced fragmentation of rivers (Saunders et al., 1991; Khan and Colbo, 2008). Barriers in the form of  
52 dams, weirs and culverts have become so prominent in today's river systems that the majority of them  
53 have lost their original connectivity and natural characteristics (Jungwirth, 1998; Jager et al., 2001).  
54 These barriers exacerbate the current poor state of many freshwater ecosystems. Efforts to mitigate the  
55 impacts of barriers, such as fishpasses, have seen limited success (Bunt et al., 2012) and are usually  
56 costly (Gibson et al., 2005). Furthermore, such approaches do not repair the damage done to the  
57 ecosystems as a whole (Birnie-Gauvin et al., 2017); rather, they provide an opportunity for *some* fish to  
58 move upstream or downstream past the barrier. This is particularly relevant for migratory fish species  
59 like salmonids, which depend on freshwater migrations to complete their lifecycle (Jonsson and  
60 Jonsson, 1993; Klemetsen et al., 2003). Better management tools need to be implemented to promote  
61 the persistence of these migratory species, such as barrier removal and other types of restoration  
62 projects.

63

### 64 *1.2 Brown trout*

65 The brown trout (*Salmo trutta*, Salmonidae) is a partially anadromous salmonid species, native to many  
66 regions of Europe (Jonsson and Jonsson, 1993). Brown trout spawn in the upper reaches of rivers,  
67 where the substrate is typically suitable for spawning and early growth, and predators are typically  
68 absent (Shirvell and Dungey, 1983; Armstrong et al., 2003). Juvenile trout generally spend between  
69 one to five years in freshwater, after which individuals differentiate phenotypically (Nielsen et al.,

2003). Some individuals will assume a resident phenotype and remain in freshwater their entire life, while others will assume the migratory phenotype and migrate to marine environments (Jonsson and Jonsson, 1993; Nielson et al., 2006). This phenomenon is known as partial migration (Chapman et al., 2011).

While the drivers for partial migration remain poorly understood (though many hypotheses exist, Chapman et al., 2011), the benefits of migrating to sea appear to be linked to a larger availability of food items in marine environments, thus allowing migratory individuals to attain larger sizes and a greater reproductive potential (Northcote, 1984; Chapman et al., 2011; Shrimpton, 2013). Juveniles that become migratory individuals are known as smolts, and differ from their resident counterparts both behaviorally and physiologically. For example, smolts appear to be less aggressive (Jonsson and Jonsson, 2011; Thorstad et al., 2012), have greater sodium-potassium ATPase activity in their gills (Aarestrup et al., 2000), and appear to have greater levels of blood-circulating antioxidants (Birnie-Gauvin et al., 2017).

Smolts typically migrate during the months of March to May depending on latitude (peak smolt migration period, e.g., Bohlin et al., 2011), though some migrate during the autumn (Aarestrup et al., 2018). The downstream smolt migration is thought to be triggered by a range of environmental factors, such as photoperiod, temperature and discharge (Hoar, 1988). Furthermore, smolts are thought to migrate downstream during the “smolt window”. This window is thought to be affected by factors such as physiological and ecological readiness to enter marine environments, risk of predation, and growth potential (McCormick et al., 1998). It is thus essential that smolts be able to reach marine waters as quickly and easily as possible, with their passage unhindered.

### *1.3 The restoration project*

93 Barriers cause the upstream portion of the river to become inundated and thus hinder the passage of  
94 smolts heading downstream due to the slowing of water (e.g., Schwinn et al., 2017) and difficulties  
95 associated with finding a safe passage route past the structure itself (e.g., Thorstad et al., 2003).  
96 Furthermore, barriers hinder the upstream passage of adult trout during their spawning migration. In  
97 Denmark, such barriers often occur in the form of weirs in conjunction with fish farms. River  
98 Villestrup (northeast Jutland, Denmark) historically had 17 fish farms. In an attempt to restore the river  
99 to its original state and reinstate connectivity on the lower two thirds of the river, six weirs (five in the  
100 mainstem and one in a tributary) were removed. All associated fish farms were simultaneously closed.  
101 The weirs were likely to have been several hundred years old, though precise years of origin are not  
102 available. Each weir was originally made of concrete or wood, and removed by digging and removing  
103 all parts of the structure completely. Each removal occurred within the course of a few days, though  
104 weirs were removed in different years. In 2004, when the restoration project began, seven weirs were  
105 left. The lower-most weir was removed in 2005, and five more were subsequently removed between  
106 2010 and 2013 (see Figure 1C for weir locations, and Table 1 for specific details on each weir). Today,  
107 only one weir remains in the upstream portion of the river (Figure 1, #6). This study investigated the  
108 effectiveness of this restoration approach with regards to the smolt run over the course of 12 years (five  
109 study years).

111 **2. Materials and Methods**

113 *2.1 Study site and trap set up*

114 River Villestrup is located in northeast Jutland (Denmark), where it runs for 20km before entering the  
115 Mariager Fjord (Figure 1). The river is fed by groundwater and rainfall, and has a mean annual

discharge of  $1.1\text{m}^3\text{ s}^{-1}$ . It is home to a wild population of partially anadromous brown trout, with both resident and migratory phenotypes. Before the weir removals, river Villestrup was characterized mostly by sandy and muddy substrates in the close vicinity of the weirs, with little pool/riffle habitat. As in most Danish rivers, river Villestrup had and still has a relatively low gradient (approx. 1.0%), and meandering form. However, following the removals, the river bed is characterized by coarse, gravelly substrates. For every study year (i.e., 2004, 2008, 2009, 2015 and 2016), a full-covering Wolf trap (8mm grid spacing; Wolf 1951) was set up 200m from the mouth of the river (Figure 1C, #1). The trap covered the entire width of the river (approx. 6m), allowing us to capture virtually every fish larger than 10 cm. The trap was in place from April 1<sup>st</sup> to May 31<sup>st</sup> every year, and was emptied daily during that period.

Unfortunately, given the expenses and time required to maintain a trap for two months, we could not perform the study continuously between 2004 and 2016. Thus, specific study years were selected to provide the most representative data to evaluate the effects of weir removal through a BACI approach.

## 2.2 Fish processing

Every day during the study period, the trap was emptied to count and measure ( $\pm 0.1\text{cm}$ ) all smolts. Fish were anesthetized with benzocaine ( $0.03\text{g l}^{-1}$ ) for measurements and fin clipped (adipose fin). Fish were then released just downstream of the trap. While it was unlikely, fish could return upstream after having been measured. In that case, fin-clipping allowed us to detect if a fish had already been measured and counted, and that individual was then removed from the day's count.

## 2.3 Environmental variables

139 Water discharge data were obtained from a monitoring station located 750m upstream of the trap.

140 Temperature data were obtained using an underwater temperature data logger (Onset HOBOTidbit v2

141 UTBI-001, range: -20°C to 70°C, Massachusetts, USA).

142

#### 143 *2.4 Data analysis*

144 All trout between 10.0 and 21.0 cm caught in the trap were considered to be smolts (despite coloration)

145 for the purpose of the analysis. This is a fair assumption given the close distance between the trap and

146 the fjord. Furthermore, a follow up electrofishing pass downstream of the trap after the end of the smolt

147 season showed very few trout. Mean length between years was compared using a simple linear

148 regression model:

$$149 \quad \log(\text{length}_i) = \text{year}_i + \varepsilon_i$$

$$150 \quad \varepsilon_i \sim N(0, \sigma^2)$$

151 Lengths were log-transformed to meet assumptions of normality and homoscedacity.

152 All statistical analyses were performed using R version 3.4.1.

153

### 154 **3. Results**

155 The size of the smolt run increased significantly following the removal of weirs, with the largest class

156 in 2015, followed by 2016 (Table 2; Fig. 2). Average length of downstream migrating trout was

157 different across study years, decreasing significantly every year (GLM,  $p < 0.05$ ; Fig. 3). We note an

158 indication of earlier peak migration following weir removal (Fig. 2 and 4).

159

### 160 **4. Discussion**

161



#### 4.1 Smolt run

The removal of low-head weirs in River Villestrup strongly increased smolt output. The removal of the most downstream weir in 2005 alone led to a large increase in smolts in 2008 and 2009, suggesting that re-establishing the ease of access to the fjord aided a large number of fish in successfully migrating to marine environments. Given that a Danish smolt cohort typically resides in freshwater for one to two years before migrating, the timeline of these observations are in line with the prediction that the effects of weir removal may take 2+ years to appear, though we do not have data for the years of 2006-2007 to demonstrate this. The subsequent removal of five more weirs led to an even greater increase in 2015 and 2016. Our results indicate that weir removal reinstated the natural habitat of the river, with many areas dominated by fast-moving water, riffles, and coarse substrate, where ponded zones previously were. These environmental changes presumably restored or even created new grounds ideal for spawning and early development which adults and fry did not have access to for centuries, when fish farms and mills were first established in the river system. Adult sea trout are also able to spawn farther upstream than when the barriers were present. Preliminary data shows a 9-fold increase in adult spawners between 2004 and 2016 (from an estimated 333 to 3700 individuals, data unpublished). Furthermore, observations also suggest that sedimentation caused by barriers may trap fry upon emergence (Rubin, 1998). The removal of obstacles would then also increase the survival of fry, and thus result in a larger smolt run. Unfortunately, our set up did not allow us to follow sediment displacement post-removal, and we cannot exclude the possibility of sediments being deposited on spawning grounds. However, observations from fisheries technicians and local anglers supported an increase in the number of spawning grounds throughout the river length, with a large increase in sea trout spawners. We therefore suggest that the increase in availability of spawning grounds may have offset the negative impacts of sediment release caused by the removals. Observations of increased

185 spawners suggest that even if sediments ended up on spawning grounds, the effects were non-  
186 problematic.

187         We observed an unexpected significant decrease in the smolt output between 2015 and 2016.  
188 Three possible explanations arise. 1. It is possible that the large smolt run from 2015 reduced the smolt  
189 output from 2016. Previous research has shown that the density of an age class of brown trout can  
190 affect one or more subsequent age classes through intraspecific competition between cohorts (Elliott,  
191 1994; Nordwall et al., 2001). In this case, the 1+ age class which migrated in 2015 may have  
192 significantly reduced the abundance of the 0+ age class which would have migrated in 2016, either  
193 through predation, density-dependent mortality or intraspecific competition (Elliott, 1994). 2. It is  
194 possible that the decrease was due to variation in the annual smolt production, which may vary from  
195 year to year due to variation in biotic and abiotic factors (Chadwick, 1982; Warren et al., 2015). In this  
196 case, we would expect the number of smolts to increase again in the upcoming years. 3. It is possible  
197 that the population suffered high overwinter mortality due to harsh environmental conditions (Elliott,  
198 1993). Other Danish streams were found to have poor overwinter survival (personal observation, K.  
199 Birnie-Gauvin, Gudsø stream).

200

#### 201 *4.2 Smolt size and peak migration*

202 We observed a decrease in the average smolt size through the years. It is possible that following weir  
203 removal, smaller fish were also successful in migrating downstream, rather than larger fish only, which  
204 are presumably more apt at escaping predators in ponded zones or overcoming weirs (Winstone et al.,  
205 1985). In other words, smaller fish no longer get stuck at weirs and/or penetrate the grid used to prevent  
206 fish from entering the water intake channel at fish farms, and are capable of descending downstream.  
207 Another possibility for progressively smaller fish following weir removal is that a greater number of

208 fish caused higher intraspecific competition for food, and may have resulted in smaller fish (Holm et  
209 al., 1990). Additionally, it is likely that spawning success and recruitment increased, which simply  
210 increased the number of migrating fish, with a wide range of sizes. Our findings likely reflect a  
211 combination of all three possible explanations. Alternatively, it is possible that the removals impacted  
212 the invertebrate community, and thus may have reduced food availability. While we cannot rule out  
213 this explanation, it is rather unlikely that the post-removal invertebrate community had diminished so  
214 much that fish were smaller in size. Because fast-flowing water is typically inhabited by different  
215 invertebrate types than slower moving water (Doisy and Rabeni, 2001), we argue that the invertebrate  
216 community *changed* rather than *diminished* post-removal.

217 We expected the peak migration to occur earlier following the removal of the weirs through a  
218 reduction in delays at ponded zones, but cannot make that conclusion for certain. While our results  
219 indicate a trend for an earlier peak migration, flood events during the study years make it impossible to  
220 make a meaningful analysis. Evidence suggests that dams delay the passage of migrating fish greatly  
221 (Aarestrup and Koed, 2003; Gauld et al., 2013), and that these effects are worse when multiple dams  
222 must be overcome (Caudill et al., 2007). Ponded zones can cause smolts to lose their orientation due to  
223 diminished flow, thus delaying them (Schilt, 2007). The removal of five of the six weirs in the main  
224 stem of river Villestrup likely prevented such delays in downstream migration, thus enabling fish to  
225 reach marine environments faster.

#### 226 227 4.3 Implications

228 Our results suggest that complete barrier removal has several important implications for  
229 freshwater fisheries and river management. Weir removal presumably increases the number of adult  
230 fish able to successfully migrate upstream and spawn, perhaps due to a reduced incidence of injuries at

231 obstacles, diminished energy expenditure to attain spawning grounds (i.e., adults no longer have to  
232 invest energy to surpass barriers), and by making impassable stretches into passable ones (Castro-  
233 Santos and Letcher, 2010). Furthermore, weir removal may increase reproductive output through  
234 successful egg emergence (i.e., unhindered by sedimentation), which would then lead to an increased  
235 recruitment rate and an increased smolt output in the following 2+ years. Weir removal also makes  
236 smolts more successful in their downstream migration via reduced mortality at fish farm intake grids  
237 (Aarestrup and Koed, 2003), reduced predation at ponded zones (Jepsen et al., 1998), decreased delays  
238 (Aarestrup and Koed, 2003; Schilt, 2007) and presumably decreased energy expenditure. In addition,  
239 barriers may induce an artificial population structure by favouring larger individuals; removal can  
240 reinstate a more natural population structure, with a wider size range.

241 Many of the fish species that migrate between freshwater and marine waters, including trout,  
242 are used as indicator species for good environmental and ecological status, as they experience the many  
243 different habitats during their movement from upland streams to lowland rivers and then to the sea  
244 (Lasne et al., 2007; Gough et al., 2012). Their importance in the context of management cannot be  
245 understated. Fish usually migrate for one of three reasons; migrations are either for spawning, feeding  
246 or refuge seeking (Northcote, 1984). Regardless of the causes for migration, barriers diminish the ease  
247 of access to spawning and feeding grounds, and hinder passage to refuge areas. These effects are likely  
248 exacerbated in rivers with numerous barriers (Lucas and Batley, 1996). Extensive fragmentation of  
249 river connectivity limits dispersal of many fish species (McLaughlin et al., 2006). Furthermore, dams  
250 impact the hydrogeomorphology of streams in some places. For example, barriers cause a decrease in  
251 water velocity, an increase in water temperature, a decrease in oxygen availability, and sedimentation  
252 (Baxter, 1977; Petts, 1984). Since most diadromous species exhibit homing behaviour, and because the  
253 latter is directly related to predictable environmental conditions such as temperature, water chemistry,

and rhythmic patterns of environmental changes, their homing behavior is likely to be greatly impacted by the presence of obstacles (Lucas and Baras, 2008).

In the present study, we demonstrate that weir removal is an appropriate approach to reinstate river connectivity and to increase long-term population sustainability of fish species. We provide some of the first data evaluating the full river system effects of barrier removal, and further emphasize the need to implement this approach in management schemes whenever possible.

## Acknowledgements

We wish to thank all technicians and volunteers for their help in the field. We also wish to thank the Danish Rod and Net Fish License Funds for providing funding to support this study. K.B.G. is funded through the AMBER project (EU #689682).

## Data

Data will be made available on figshare upon acceptance of the manuscript.

## Literature Cited

Aarestrup, K., Nielsen, C. & Madsen, S.S. (2000). Relationship between gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 2086-2095.

275 Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon  
 276 (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, 12, 169-  
 277 176.  
 278  
 279 Aarestrup, K., Birnie-Gauvin, K. & Larsen, M.H. (2018). Another paradigm lost? Autumn downstream  
 280 migration of juvenile brown trout: evidence for a presmolt migration. *Ecology of Freshwater Fish*, 27,  
 281 513-516.  
 282  
 283 Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. (2003). Habitat requirements  
 284 of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, 62,143-170.  
 285  
 286 Baxter, R.M. (1977). Environmental effects of dams and impoundments. *Annual Review of Ecology*  
 287 *and Systematics*, 8, 255-283.  
 288  
 289 Birnie-Gauvin, K., Aarestrup, K., Riis, T.M.O., Jepsen, N. & Koed, A. (2017). Shining the light on the  
 290 loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers and its  
 291 implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27, 1345-  
 292 1349.  
 293  
 294 Birnie-Gauvin, K., Peiman, K.S., Larsen, M.H., Baktoft, H., Aarestrup, K., Willmore, W.G. & Cooke,  
 295 S.J. (2017). Oxidative stress and partial migration in brown trout (*Salmo trutta*). *Canadian Journal of*  
 296 *Zoology*, 95, 829-835.  
 297

298 Bohlin, T., Dellefors, C. & Faremo, U. (1993). Timing of sea-run brown trout (*Salmo trutta*) smolt  
 299 migration: effects of climatic variation. *Canadian Journal of Fisheries and Aquatic Sciences*, 50, 1132-  
 300 1136.  
 301  
 302 Bunt, C.M., Castro-Santos, T. & Haro, A. (2012). Performance of fish passage structures at upstream  
 303 barriers to migration. *River Research and Applications*, 28, 457-478.  
 304  
 305 Castro-Santos, T. & Letcher, B.H. (2010). Modeling migratory energetics of Connecticut River  
 306 American shad (*Alosa sapidissima*): implications for the conservation of an iteroparous anadromous  
 307 fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 806-830.  
 308  
 309 Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J., Zabel, R.W.,  
 310 Bjornn, T.C. & Peery, C.A. (2007). Slow dam passage in adult Columbia River salmonids associated  
 311 with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent  
 312 mortality?. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 979-995.  
 313  
 314 Chadwick, E.M.P. (1982). Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in  
 315 Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1496-1501.  
 316  
 317 Chapman, B.B., Brönmark, C., Nilsson, J.Å. & Hansson, L.A. (2011). The ecology and evolution of  
 318 partial migration. *Oikos*, 120, 1764-1775.  
 319

320 Doisy, K.E. & Rabeni, C.F. (2001). Flow conditions, benthic food resources, and invertebrate  
 321 community composition in a low-gradient stream in Missouri. *Journal of the North American*  
 322 *Benthological Society*, 20, 17-32.

323

324 Elliott, J.M. (1993). A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English  
 325 Lake District stream. *Production of juvenile Atlantic salmon, Salmo salar, in natural waters*. (eds R.J.  
 326 Gibson & R.E. Cutting), pp. 109-122. Canadian Special Publication of Fisheries and Aquatic Sciences,  
 327 Ottawa.

328

329 Elliott, J.M. (1994). *Quantitative ecology and the brown trout*. Oxford University Press, Oxford.

330

331 Gauld, N.R., Campbell, R.N.B. & Lucas, M.C. (2013). Reduced flow impacts salmonid smolt  
 332 emigration in a river with low-head weirs. *Science of the Total Environment*, 458, 435-443.

333

334 Gibson, R.J., Haedrich, R.L. & Wernerheim, C.M. (2005). Loss of fish habitat as a consequence of  
 335 inappropriately constructed stream crossings. *Fisheries*, 30, 10-17.

336

337 Gough, P., Philipsen, P., Schollema, P.P. & Wanningen, H. (2012). *From sea to source; International*  
 338 *Guidance for the Restoration of Fish Migration Highways*. Regional Water Authority Hunze en Aa's,  
 339 Netherlands.

340

341 Hoar, W.S. (1988). 4. The Physiology of Smolting Salmonids. *Fish physiology*, 11, 275-343.

342



343 Holm, J.C., Refstie, T., & Bø, S. (1990). The effect of fish density and feeding regimes on individual  
 344 growth rate and mortality in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, 89, 225-232.  
 345

346 Jager, H.I., Chandler, J.A., Lepla, K.B. & Van Winkle, W. (2001). A theoretical study of river  
 347 fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of*  
 348 *Fishes*, 60, 347-361.  
 349

350 Jepsen, N., Aarestrup, K., Økland, F. & Rasmussen, G. (1998). Survival of radiotagged Atlantic salmon  
 351 (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward  
 352 migration. *Hydrobiologia*, 371, 347-353.  
 353

354 Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in  
 355 fishes. *Reviews in Fish Biology and Fisheries*, 3, 348-365.  
 356

357 Jonsson, B., and Jonsson, N. (2011). Ecology of Atlantic salmon and brown trout: habitat as a template  
 358 for life histories. Springer, Dordrecht.  
 359

360 Jungwirth, M., Schmutz, S. & Weiss, S. (1998). *Fish Migration and Fish Bypasses*. Fishing News  
 361 Books, Oxford.  
 362

363 Khan, B., & Colbo, M. H. (2008). The impact of physical disturbance on stream communities: lessons  
 364 from road culverts. *Hydrobiologia*, 600, 229-235.  
 365

366 Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'connell, M.F. &  
 367 Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr  
 368 *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12, 1-59.  
 369  
 370 Lasne, E., Bergerot, B., Lek, S. & Laffaille, P. (2007). Fish zonation and indicator species for the  
 371 evaluation of the ecological status of rivers: example of the Loire basin (France). *River Research and*  
 372 *Applications*, 23, 877-890.  
 373  
 374 Lucas, M.C. & Batley, E. (1996). Seasonal movements and behaviour of adult barbel *Barbus barbus*, a  
 375 riverine cyprinid fish: implications for river management. *Journal of Applied Ecology*, 33, 1345-1358.  
 376  
 377 Lucas, M. & Baras, E. (2008). *Migration of Freshwater Fishes*. Blackwell-Science, Oxford.  
 378  
 379 McCormick, S.D., Hansen, L.P., Quinn, T.P. & Saunders, R.L. (1998). Movement, migration, and  
 380 smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55,  
 381 77-92.  
 382  
 383 McLaughlin, R.L., Porto, L., Noakes, D.L., Baylis, J.R., Carl, L.M., Dodd, H.R., Goldstein, J.D.,  
 384 Hayes, D.B. & Randall, R.G. (2006). Effects of low-head barriers on stream fishes: taxonomic  
 385 affiliations and morphological correlates of sensitive species. *Canadian Journal of Fisheries and*  
 386 *Aquatic Sciences*, 63, 766-779.  
 387

388 Nielsen, C., Aarestrup, K., Nørum, U. & Madsen, S.S. (2003). Pre-migratory differentiation of wild  
389 brown trout into migrant and resident individuals. *Journal of Fish Biology*, 63, 1184-1196.

390

391 Nielsen, C., Aarestrup, K. & Madsen, S.S. (2006). Comparison of physiological smolt status in  
392 descending and nondescending wild brown trout (*Salmo trutta*) in a Danish stream. *Ecology of*  
393 *Freshwater Fish*, 15, 229-236.

394

395 Nordwall, F., Näslund, I. & Degerman, E. (2001). Intercohort competition effects on survival,  
396 movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of*  
397 *Fisheries and Aquatic Sciences*, 58, 2298-2308.

398

399 Northcote, T.G. (1984). Mechanisms of Fish Migration in Rivers. *Mechanisms of Migration in*  
400 *Fishes* (eds. J.D. McCleave, G.P. Arnold, J.J. Dodson, W.H. Neill), pp. 317-355. Springer, New York.

401

402 Petts, G.E. (1984). *Impounded Rivers: Perspectives for Ecological Management*. John Wiley,  
403 Chichester.

404

405 Rubin, J.F. (1998). Survival and emergence pattern of sea trout fry in substrata of different  
406 compositions. *Journal of Fish Biology*, 53, 84-92.

407

408 Saunders, D. A., Hobbs, R. J. & Margules, C. R. (1991). Biological consequences of ecosystem  
409 fragmentation: a review. *Conservation Biology*, 5, 18-32.

410

411 Schilt, C.R. (2007). Developing fish passage and protection at hydropower dams. *Applied Animal*  
 412 *Behaviour Science*, 104, 295-325.  
 413  
 414 Schwinn, M., Aarestrup, K., Baktoft, H. & Koed, A. (2017). Survival of migrating sea trout (*Salmo*  
 415 *trutta*) smolts during their passage of an artificial lake in a Danish lowland stream. *River Research and*  
 416 *Applications*, 33, 558-566.  
 417  
 418 Shirvell, C.S. & Dungey, R.G. (1983). Microhabitats chosen by brown trout for feeding and spawning  
 419 in rivers. *Transactions of the American Fisheries Society*, 112, 355-367.  
 420  
 421 Shrimpton, J.M. (2013). Seawater to freshwater transitions in diadromous fishes. *Fish Physiology:*  
 422 *Euryhaline Fishes* (eds S.D. McCormick & C.J. Brauner), pp.327-393. Academic Press, Oxford.  
 423  
 424 Thorstad, E.B., Økland, F., Kroglund, F. & Jepsen, N. (2003). Upstream migration of Atlantic salmon  
 425 at a power station on the River Nidelva, Southern Norway. *Fisheries Management and Ecology*, 10,  
 426 139-146.  
 427  
 428 Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. (2012). A  
 429 critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial  
 430 post-smolt migration. *Journal of Fish Biology*, 81, 500–542.  
 431  
 432 Warren, M., Dunbar, M.J., & Smith, C. (2015). River flow as a determinant of salmonid distribution  
 433 and abundance: a review. *Environmental Biology of Fishes*, 98, 1695-1717.

434

435 Winstone, A.J., Gee, A.S. & Varallo, P.V. (1985). The assessment of flow characteristics at certain  
436 weirs in relation to the upstream movement of migratory salmonids. *Journal of Fish Biology*, 27, 75-  
437 83.

438

439 Wolf, P. (1951). A trap for the capture of fish and other organisms moving downstream. *Transactions*  
440 *of the American Fisheries Society*, 80, 41-45.

441

442

443

444

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462

463

464

465

466

467

468

469

470

471

472  
473  
474  
475  
476

**Table 1. Weirs in River Villestrup.** Height (m), width (m), length of ponded zones (m), presence or absence of fishway and date of removal for the weirs found in River Villestrup.

Weir #	Height (m)	Width (m)	Length of ponded zone (m)	Fishway present?	Year of removal
1	1.9	5.9	800	Yes	2005
2	1.8	4.1	180	Yes	2012
3	0.1	5.6	0	Yes	2012
4	1.8	2.7	600	Yes	2012
5	1.5	5.0	600	Yes	2012
6	1.8	4.8	900	No	Not removed
7	1.0	1.7	500	Yes	2012

477  
478  
479  
480  
481  
482  
483  
484  
485  
486  
487  
488  
489  
490  
491  
492  
493  
494  
495  
496  
497  
498  
499  
500  
501  
502  
503  
504  
505  
506

**Table 2. Smolt output.** Average length of brown trout (*Salmo trutta*), average daily count, total count and most caught in a single day for each study year.

	<b>2004</b>	<b>2008</b>	<b>2009</b>	<b>2015</b>	<b>2016</b>
<b>Average length (cm)</b>	16.3±3.0	15.5±4.2	14.5±23.6	13.3±2.4	13.2±2.2
<b>Average daily count</b>	27.2	75.4	82.6	312.9	134.2
<b>Total count</b>	1660	4598	5038	19105	8185
<b>Most in a day</b>	92	931	263	5214	1853

539

## 540 **Figure Captions**

541

542 **Figure 1. Map of River Villestrup.** River Villestrup is situated in northeastern Jutland, Denmark (A).  
543 It runs for approximately 20 km before entering the Mariager Fjord (B). A total of 7 weirs were present  
544 in the system originally; 6 were removed, with one still remaining (#6, C).

545

546 **Figure 2. Catch per day.** Number of downstream migrating brown trout (*Salmo trutta*) smolts and  
547 discharge ( $\text{m}^3 \text{s}^{-1}$ ) in River Villestrup between April 1 and May 31, for years 2004 (A), 2008 (B), 2009  
548 (C), 2015 (D) and 2016 (E). Note variable scale on Y-axis.

549

550 **Figure 3. Length distribution.** *Left:* Length distributions of downstream migrating brown trout (*Salmo*  
551 *trutta*). Red dots and intervals indicate mean length  $\pm$  SD. *Right:* Visualisation of the fitted model. Estimated  
552 mean length and associated 95 % confidence intervals (back-transformed to original scale). Mean log (length)  
553 were significantly different between all years ( $p < 0.05$ ).

554

555 **Figure 4. Migration timing.** Cumulative migration curve for brown trout (*Salmo trutta*) smolts for  
556 each study year.

557

558

559

560